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Abstract

Weight loss and dynamics of plant nutrients (N, P, K, Ca, Mg, S, Fe, Mn, Na, Zn and Cu) in leaf litter were studied in a mature beech forest in South Sweden, using the litter bag technique. An initial decomposition period of about 12 to 18 months was characterized by an absolute net increase of N, P, and S contents in litter, followed by a period of net release of these elements. This development, which was most obvious for N and P, was interpreted as a change from a phase where decomposer activity was limited by the availability of nutrient elements to an energy-limited phase. A net release of nitrogen did not occur until after two years of decomposition, and a transfer of nitrogen and phosphorus between different litter layers is here proposed to work as a retention mechanism.

Potassium and sodium were quickly leached from the litter, while release of magnesium, calcium, and initially also manganese, was more associated to organic matter weight loss. Iron, zinc and copper were all strongly accumulated in the litter material. This is explained by mineral soil admixture for the former element and by atmospheric fall out in combination with the chemical complex formation character for the latter two elements.

Finally the importance of the different release processes in the total nutrient recycling of the forest is discussed.

1. Introduction

Nutrient release from plant and animal debris is a fundamental process of nutrient recycling in natural ecosystems. Together with transports in the soil solution and immobilization by soil organisms, including plant roots, it regulates the turnover rate and distribution of bioelements in soil. The litter and its decomposition is thereby important for the overall nutrient regime of an ecosystem and for a continuous plant production.

Most studies of decay and bioelemental change of different litter types have utilized the litter bag technique (see e.g. Gilbert & Bock 1960, Bock 1963, Attiwill 1968, Wood 1974). It will give a satisfactory image of the process in litter if the mesh of the bags is kept wide enough for entry of soil fauna and if fragmental loss of material is controlled (Suffling and Smith 1974). Towpasz (1976) found that beech litter decomposition in litter bags with a mesh size of 2 mm corresponded well to that of non-confined litter, while for other deciduous trees it gave values that were too low.

The elemental composition of substrate-decomposer systems, measured as carbon/element ratio, usually varies considerably during decay, indicating different rates of release compared to that of carbon. Initial leaching of sodium and potassium often causes a rapid loss of these elements (Kucera 1959, Frankland 1966). A critical C/element ratio is required before a net loss from the system of certain elements can be detected. This is reported, for example, for nitrogen (see Black 1968), phosphorus (see Cosgrove 1967) and sulphur (Stewart *et al.* 1966). A net gain during certain stages of decomposition of forest litter is well established for nitrogen (Gilbert and Bock 1960, Bock 1963, Anderson 1973, Howard and Howard 1974, Wood 1974, Staaf and Berg 1977), but sometimes for other elements as well. Gosz *et al.* (1973) found absolute increases in N, P, S, Zn, Fe and Cu during various periods of first-year decomposition of some leaf litters, and Will (1967) found the same for N and Mg in needle litter.

The aims of the present investigation are to study the absolute and rela-

tive changes of carbon and some essential plant nutrients in decomposing beech leaf litter in a South Swedish beech forest, to detect some of the mechanisms involved and make conclusions about their role in the nutrient economy of the forest ecosystem.

2. Site description

The investigation was performed in Kongalund, a beech (*Fagus silvatica* L.) forest area in South Sweden (55° 59' N, 13° 10' E). Its general appearance, tree biomass, production, and mineral cycling have earlier been dealt with by Nihlgård (1970, 1972) and Nilsson (1978). The rock is cambrian shales and sandstones, which is covered by a thick layer of moraine; mainly of acid siliceous origin. Acid brown forest soils are typical of the area. The mean annual temperature is 6-7°C, and the yearly precipitation about 800 mm.

The experimental area was situated in a 100-year-old beech stand (tree density, 120 trees/ha⁻¹), with a field layer dominated by *Lamium galeobdolon* L., *Stellaria nemorum* L., *Anemone nemorosa* L., and *Milium effusum* L. On top of the brown forest soil is a well developed A₀ horizon and a rather thin mull layer with a pH in water extract of about 4.5. Sand is the dominating textural component, and the clay content is less than 10 per cent of weight.

3. Methods

3.1 Collection and preparation of samples

Newly fallen leaves were collected from nylon nets placed just above the ground at eight places (2 x 2 m) in the beech stand in late October 1971. They were pooled to one composite sample and stored in a plastic bag for two days in order to level out moisture differences within it. Leaf material corresponding to 12.0 g dry weight was put in each nylon bag with 8 mm mesh size, sized 20 cm by 20 cm. The litter weight per area covered by bags corresponded roughly to that of annual leaf fall in the forest (Nihlgård 1972, Nilsson 1978). Totally eighty-four bags were put in the upper litter layer of six 5 x 5 m blocks within the experimental site, sized 50 x 50 m. One randomly chosen bag from each block was collected on 16 occasions during a two and a half year period. During the summer of 1973

the site was defoliated by an invading larvae population of *Dasychira punibunda* L. (Lepidoptera). (Nilsson 1978).

In the laboratory obvious non-original particles and visible dead or living animals were removed from the litter samples. They were then dried at 85°C, weighed and analyzed for total concentrations of C, N, P, K, S, Ca, Mg, Na, Fe, Mn, Zn and Cu.

Water-extractions were made on one composite samples from litter bag sets collected after 0, 6, 12, 18, 24 and 30 months of incubation. Two grams of dried and milled (particle size < 1.5 mm) leaf material were extracted in 100 ml demineralized water for 10 hours in a shaker. All the above-mentioned elements except carbon were analyzed on the filtered extracts and pH was measured in the unfiltered liquid residue.

The mineral soil horizon 0-5 cm (A_1) was sampled with a steel cylinder. Twenty samples were taken in a randomized way within the investigation area in spring 1972. Roots were sorted out, and after sieving through a 2 mm mesh net, the fine earth was analyzed for total carbon and nitrogen.

The litter layer A_0 was not sampled until late spring 1976 in a nearby stand of very similar appearance to the original one. It was used because the original stand had now been felled. In 26 systematically placed areas of 0.07 m² each, the litter layer, including A_0 , were collected and assorted; only leaf litter being retained. The samples were pooled to one composite sample, and analyzed for ash content and total content of all the elements mentioned above.

3.2 Chemical methods

Double analyses were consistently used on all samples. Carbon was determined by wet oxidation (Nömmik 1971), and nitrogen by traditional semi-micro Kjeldahl procedure. After an acid wet oxidation in $\text{HNO}_3 + \text{HClO}_4$ the following analyses were performed; a turbidimetric analysis for sulphur as BaSO_4 -precipitate (Blanchar *et al.* 1965), a vanadate-yellow-complex method (Jackson 1958) for phosphorus and a flame photometric procedure for sodium and potassium. Calcium, magnesium, iron, manganese, zinc, and copper were all determined by atomic adsorption spectrophotometry (Perkin-Elmer 403) against acid standards. For calcium and magnesium the analyses were made in 1% LaCl -solution (Pawluk 1967).

The leaf litter extracts were divided in two parts. One part was analyzed for nitrogen with an ammonia-selective electrode (Orion 95-19) after oxidation of 25 ml of the extract in 1 ml H_2SO_4 and $\text{K}_2\text{SO}_4 + \text{CuSO}_4$ catalyst, evaporation and dilution. Another 50 ml was evaporated, oxidized in 5 ml $\text{HNO}_3 + \text{HClO}_4$, excess acid evaporated, diluted and analyzed for the same elements as the litter samples. Triple analyses were performed on all extraction samples.

3.3 Calculations

All incubated litter samples were analyzed individually for their content of the different elements, and calculations of concentrations and total amounts were primarily made on an individual sample basis. Mean values of the mentioned variables for each collection were generally given with 95% confidence limits, assuming approximate normal distribution of measured attributes.

4. Results and discussion

4.1 Release and accumulation of plant nutrients in litter

Nitrogen, phosphorus and sulphur

All these elements showed similar trends expressed as relative changes in the amount remaining in the litter (Fig. 1). A steady accumulation during 8-14 months, possibly with a small loss during the initial period, was followed by a successive loss period. Nitrogen and phosphorus decreased at about the same rate as organic matter, although phosphorus was released significantly faster during the latest period, and diverged a bit from the other elements also in the detailed time development.

The sizes of the water-soluble fractions of nitrogen, phosphorus and sulphur in litter at leaf fall (Table 1) were in good agreement with the amounts of these elements lost during the first month in the field (Fig. 1). This makes mechanical leaching of inorganic or organic compounds (cf. Nykvist 1962) the most probable release mechanism during this initial period. A very small decrease in nitrogen, not indicated in Figure 1, was observed already after five days of field incubation, but otherwise the initial loss of this element was smaller than for the others.

After the initial leaching period only very small amounts were currently water-soluble. This, together with the fact that nitrogen, phosphorus and sulphur are covalently bound in organic compounds, makes mineralization and subsequent leaching the most probable mechanism for release of these elements during the rest of the decomposition period.

One month after leaf fall the measured C/N, C/P and C/S ratios in the leaves were 46, 352 and 476 respectively. These values are high compared to those given in the literature on the maximum ratios for net mineralization to occur from a decomposing substrate; 15-33 for nitrogen (Black 1968), 200 for phosphorus (Cosgrove 1967) and 200-400 for sulphur (Freney 1967). Parnas (1975) theoretically examined a decomposer system where either carbon or nitrogen were the potentially limiting substances for microbial production. Among other things the results showed that in a nitrogen-limited system the C/N ratio of a decomposing substrate will decrease with time until a certain "critical" level is reached. Then the C/N ratio becomes constant with a simultaneous onset of nitrogen mineralization. Such threshold points seem possible to identify for both nitrogen, phosphorus and sulphur in the present investigation after 8-14 months of decomposition (Fig. 2).

For the beech leaf litter "critical" ratios, *sensu* Parnas, of element composition could be calculated by introducing the following assumptions: a. the litter is considered as one homogeneous substrate, b. the concentration of elements in decomposer population biomass is constant, and c. the decomposer production/assimilation efficiency is constant over time. The biomass concentrations of carbon, nitrogen and phosphorus were set to 45, 3.7 and 0.7% of dry weight respectively (Bååth and Söderström 1977); figures applying to fungi, the sulphur content to 0.4% (Ausmus and Witkamp 1974) and the production/assimilation ratio to 0.4 (Heal and MacLean 1975). This gives a need of $\frac{45}{0.4 \cdot 100} = 1.13$ weight units of carbon for each unit of biomass produced, but only 0.037 units of, for example, nitrogen. A balanced substrate, thus, should be characterized by C/N, C/P and C/S ratios of 31, 161 and 283 respectively. These figures fit well with those found in litter at the threshold points that were identified for the three elements (see Table 2 and Fig. 2). From this discussion one might draw the conclusion that during an initial phase, extended over about one year, the decomposition of beech litter was limited by the availability

of nitrogen, phosphorus, and somewhat later even sulphur in the litter; during the rest of the studied period it was carbon(energy)-limited.

An import of all three elements was noticed during the first phase, and the similar course of change indicates the presence of a biological mechanism; apart from nitrogen fixation (cf. e.g. Bocock 1963, Tchagina *et al.* 1968). The sudden loss of phosphorus during late summer and autumn 1972 is difficult to explain satisfactorily. A succession of micro-organisms is known to occur on deciduous leaf litter (Jensen 1974), and the possibility of a sudden change to populations with lower phosphorus demand is a hypothetical explanation.

Potassium and sodium

These elements are present in plant residues as water-soluble salts (Alexander 1961) and thus, are exposed to mechanical leaching when cell membranes are destroyed. The first month after leaf fall was also characterized by a loss of more than half of the initial amounts of these elements (Fig. 1). Consistently high water-soluble shares in the milled samples (Table 1) indicate that the release is effected by physical breakdown of litter structures resulting from microbial or animal activity. This is supported by the close relation between the loss of organic matter and that of potassium. During October-November 1972 there was a peak in the potassium content of the leaf litter, which coincided with the litter fall period and leaching of the fresh litter. The fact that this peak could not be found for sodium must be contributed to the slightly lower adsorption tendency for this ion compared to potassium (Ulrich 1960). This tendency might also explain the decreased C/K ratio in the A₀₁ litter horizon (Table 2), with its probably better adsorption capacity.

Calcium

Calcium is present in plant tissues in the form of calcium ions or insoluble salts in the vacuoles but it is firmly bound as calcium-pectates in the cell walls (Sailsbury and Ross 1969). Mobilizing processes will then comprise either direct leaching or ion exchange, solubilization, chelate formation or decomposition of pectates followed by leaching. Olsen (1948) found that about 60% of the calcium was bound to oxalate and about 25% was in an ion form in beech leaves at leaf fall. In Kongalund the first year of decomposition was characterized by a somewhat accelerated loss of calcium,

compared to organic matter, and in the second year the opposite situation prevailed (Fig. 1). This result fits well with Olsen's data if the structurally bound calcium is thought to be more immobile in litter and more slowly mobilized than the non-bound calcium. A close relation to the weight loss of organic matter was the general trend for calcium loss from beech leaf litter. This has been observed for other litter types eg. *Quercus*, *Acer*, *Liriodendron* leaves in both terrestrial and aquatic environments (Thomas 1970).

Magnesium

Magnesium is generally more mobile in plant tissues than calcium, and often exposed to considerable leaching (Turkey 1970). Olsen (1948) found that only about 25% of the total amount in beech leaves was organically bound at leaf fall. This, together with the fact that magnesium salts are generally rather water-soluble, makes leaching losses probable during the initial decomposition period. In this case the first year losses were greater than those for calcium, but the remaining amounts after two years were very similar (Fig. 1). A peak in November 1972, and also in November 1973, indicates leaching from newly fallen litter. Gosz *et al.* (1973) found a critical C/Mg ratio of 900-1350 above which no net release from litter occurred. Here the ratio was well below those figures during the whole investigation period (Table 2), and no accumulation could be contributed to immobilization.

Manganese

The dynamic of manganese in litter was only weakly related to that of calcium during the first year of decomposition, and thereafter an increased retention of the element was observed (Fig. 1). In the later stages both the general accumulation as well as the detailed course of element change seemed to be closely related to the pH changes in the substrate (Fig. 3).

Manganese is not a structural component of plant tissue and it exists in several oxidation states; the reduced form being the most soluble. Here the increased pH in litter might have caused a transformation of the element to an oxidized form, thus retarding the relatively rapid release in the beginning and at the very end of the incubation period. The latter period was also characterized by a marked increase in water-solubility of the element (Table 2).

Iron

There was a net gain of this element up to 45% of the initial amount during a two-year period (Fig. 1). In this forest the amount of iron in throughfall is very low (Nihlgård unpubl.), and since the variation of concentrations is very great (cf. the large confidence limits) between individual litter bags it probably originates from the underlying soil. Litter concentrations were initially very low and a transport of small mineral particles by soil animals might very well have caused this increase. In plants iron is very immobile and largely complexed to proteins (Sailsbury and Ross 1969), which might explain how it was retained. Only small amounts in litter were water-soluble (Table 2).

Beech leaves are known to have high polyphenol content, the water-soluble part of which is lost during the first four weeks after leaf fall (Andersson 1973). In addition, polyphenolic substances in canopy drip, as well as aqueous extracts of beech leaf litter, have been shown to be able to mobilize iron by complexing (Malcom and McCracken 1968); newly fallen leaves being the most effective (King and Bloomfield 1968). The action of such compounds might explain the retarded accumulation in late summer and autumn 1973 (Fig. 1).

Zinc_and_copper

These elements are both needed in small quantities by plants (Sailsbury and Ross 1969), and their solubilities in soil and litter are greatly influenced by pH, adsorption and complexing to organic matter (Ehrlich 1971). Zinc complexes are generally more water-soluble than those of copper, which make zinc the most mobile element.

In the beech leaves the contents of zinc and copper at leaf fall were 40 ppm and 5 ppm respectively, and the absolute amounts in the bags increased to about 250% for copper and 200% for zinc of the initial levels in one year (Fig. 1). During this period up to the next leaf litter fall, the leaves were exposed to atmospheric fallout. The field method permits an approximative quantification of the bio-element dynamic on an areal basis. With a leaf fall of about 3000 kg/ha in 1971 (Nilsson 1978), the first year accumulation would mean an import of 15 g Cu/ha and 120 g Zn/ha. In a nearby stand of Norway spruce about 700 g Zn/ha reached the ground in throughfall during 1973 (Nihlgård unpubl.), and Rühling and Tyler (1971) calculated the annual deposition on an open mire, less than 30 km from this forest,

to approximately 600 g Zn/ha and 30 g Cu/ha. A deposition rate of that magnitude would well explain the metal accumulation in the litter and even permit a certain loss during the first year, especially of zinc.

4.2 Plant nutrient balance in the litter layer

During the winter 1973/74 there was an evident structural change of the decomposing leaves. They became increasingly pale, fragmented and matted together, and in spring 1974 they were subjectively judged as transferred from the A_{00} to the A_{01} horizon. Knowing this point of time the element composition of the litter at different stages during its whole time span could be given (Table 2). The residence time for the leaf litter in the A_{01} layer was not known, however, but assumption of a constant fractional decay rate would give it a figure of 2.5-3.0 years.

With present results and figures for litter fall in 1971 (Nilsson 1978) and nutrient amounts in throughfall during 1967-68 in a nearby similar stand (Nihlgård 1970) a budget of N, P, K, Ca, Mg and S transfers in beech leaf litter during the first two years of decomposition at the Kongalund site could be constructed (Table 3). As the measurements are from different years and nutrients in throughfall are likely to interact with other litter types than leaves the estimate must be considered rough and only valid for interpreting general tendencies.

The budget shows that almost 20 kg nitrogen ha^{-1} were immobilized into leaf litter/decomposers during the first year of decomposition, and that only a minor part of this quantity could have been met by amounts in throughfall. Additional nitrogen supply was here supposed to come from the underlying litter generation. With this assumption the budget was almost balanced after two years of decomposition, and a net release from the leaf litter was not to be expected until the third year.

Other litter types might have functioned as nitrogen sources too. However, this possibility is not very realistic since tree litter fall other than leaves totalled 24.9 kg N ha^{-1} during 1972 (Nilsson 1978), and the field vegetation was very sparse at the research site. The amount in pollen rain ought to be included in throughfall-nitrogen. Moreover, Remacle and Vanderhorn (1973) found nitrogen fixation to have an insignificant influence on the nitrogen content of beech leaf litter from a nutrient-poor site during incubation for eight months. A transport of such great

quantities as mentioned above by migrating soil animals is also very unlikely. Thus, it seems as if either diffusion in the water phase or translocation by fungal hyphae from below can explain the implied nitrogen transport.

Phosphorus immobilization was less extensive and the phosphorus balance was positive already after the first year (Table 3). The small amounts of this element in throughfall indicate the action of a transport mechanism from an external source similar to that for nitrogen, while the immobilized sulphur was probably supplied from the vast amounts in wet deposition.

Of the other elements in the budget, potassium was mainly mobilized in the A_{01} horizon, while calcium and magnesium were more effectively retained in the litter. All these elements, however, had strongly positive balances for the first two leaf litter generations because of the relatively high rates of atmospheric deposition.

4.3 Litter decomposition in the nutrient cycling of the Kongalund forest
The present results suggest that the release rate of plant nutrients from beech leaf litter is mainly determined by:

- a) how and where the nutrient element is chemically bound in the litter
- b) the element composition of the litter in relation to decomposer need.

These two factors explain the rapid and considerable initial release of potassium and sodium. The litter morphology together with element concentrations should regulate the amounts released initially, while the overall decomposition rate determines the mobilization rate in later phases. Regarding the amounts deposited on the ground in the water phase it can be concluded, however, that biological decomposer activity is of minor importance in recycling these elements in the forest. The same can be said about sulphur, even if this element is obviously retained by microorganisms in decomposing litter.

Calcium and magnesium are more coupled to organic matter as carrier substance than those mentioned above, and here the decomposition process is important in the internal nutrient cycle of the forest. This is

especially important since the relatively large input from throughfall derives from aerosols (Nihlgård 1970).

Manganese is also associated with organic matter, but the importance of decomposers in the mobilization is still not clear, as is also the case for zinc and copper. Uptake of manganese in plants and the extractable amounts in soil seem largely to be explained by the pH of the substrate (Nihlgård and Lindgren 1977, Tyler 1976), to which decomposer activity only partly contributes.

Litter formation is the dominant input to the forest soil of nitrogen and phosphorus, which are mainly released from organic matter by biological mineralization. Present data indicates that sub-optimum concentrations in litter of these elements made decomposers retain and even incorporate them during the initial 1-1.5 years of decomposition. Thus, the hypothesis might be formulated that nitrogen and/or phosphorus release into a plant-available form from a litter which is poor in either or both of these elements is delayed in relation to the mineralization of carbon; the lower the initial concentrations of the elements the longer the delay. Further, immobilization in litter is a possible mechanism in preventing nutrient losses from soil during periods of low root activity as proposed by Ausmus *et al.* (1976) for a Liriodendron forest.

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Table 1. Total concentrations (mg g^{-1} dry weight) and amounts of water-soluble (per cent of total concentration) bioelements in beech leaves after different periods of decomposition. The measurements started on Oct. 28, 1971. * stands for not determined.

Months of decomposition	Component	C	N	P	K	Ca	Mg	S	Na	Mn	Fe	Zn	Cu
0	Total conc.	474	9.5	1.4	2.3	7.4	1.2	1.3	1.0	1.9	0.2	0.04	0.005
	Soluble	*	4	4	48	4	18	42	50	12	2	13	0
6	Total conc.	485	13.2	1.8	1.1	6.3	0.7	1.1	0.2	1.5	0.3	0.07	0.008
	Soluble	*	2	2	17	2	7	*	5	5	0	13	0
12	Total conc.	478	18.8	1.3	1.4	9.0	1.2	2.0	0.3	2.6	0.7	0.14	0.011
	Soluble	*	*	7	26	5	11	*	9	16	2	18	0
18	Total conc.	463	18.7	1.5	0.6	8.0	0.8	*	0.3	2.5	1.0	0.14	0.022
	Soluble	*	2	3	22	2	7	*	8	5	2	15	0
24	Total conc.	462	21.5	1.2	0.7	9.2	1.4	2.1	0.4	5.6	1.4	0.16	0.026
	Soluble	*	4	6	17	8	14	*	10	22	4	38	0
30	Total conc.	461	22.0	1.1	0.8	7.2	1.1	1.7	0.1	4.0	1.4	0.16	0.018
	Soluble	*	1	6	30	12	32	19	8	40	16	68	0

Table 3. A nutrient (N, P, K, Ca, Mg, S, Mn, Na) budget for the first two years of beech leaf decomposition at Kongalund. The output figures are calculated from the litter bag measurements, and the input to the second year includes both amounts transferred in organic matter and the water phase.

Decomposition period	N	P	K (kg/ha)	Ca	Mg	S	Mn	Na
<u>First year</u>								
<u>Input</u>								
Litterfall ¹⁾	36	2.7	8	19	3.3	3	6	1.9
Throughfall ²⁾	4	0.3	10	9	3.0	15	2	14
<u>Output</u>								
In litter	54	1.8	4	17	2.5	3	6	0.4
Release	-14	+1.2	+14	+11	+3.8	+15	+2	+15.5
<u>Second year</u>								
<u>Net input</u>	40	3.0	18	28	6.3	18	8	15.9
<u>Output</u>								
In litter	41	1.2	1	12	1.9	2	9	0.4
Release	-1	+1.8	+17	+16	+4.4	+16	-1	+15.5

1) From Nilsson (1978)

2. N, P, K-figures are from Nilsson (1978), and for all other elements from Nihlgård (1972).

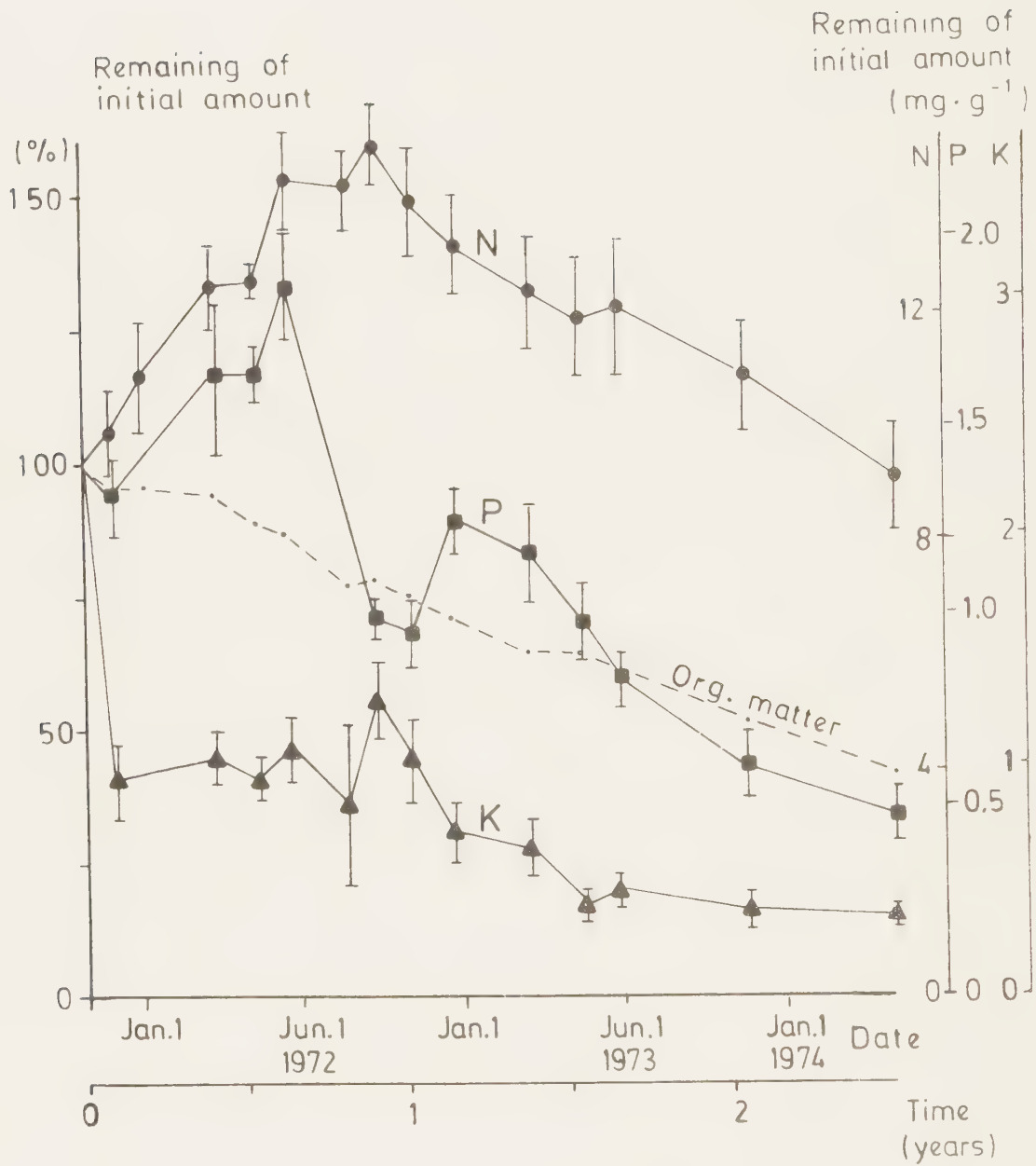


Figure 1. Absolute and relative changes of nutrient amounts in decomposing beech leaf litter at Kongalund. The dashed line showing loss of organic matter in the litter bags is identical in all three graphs.

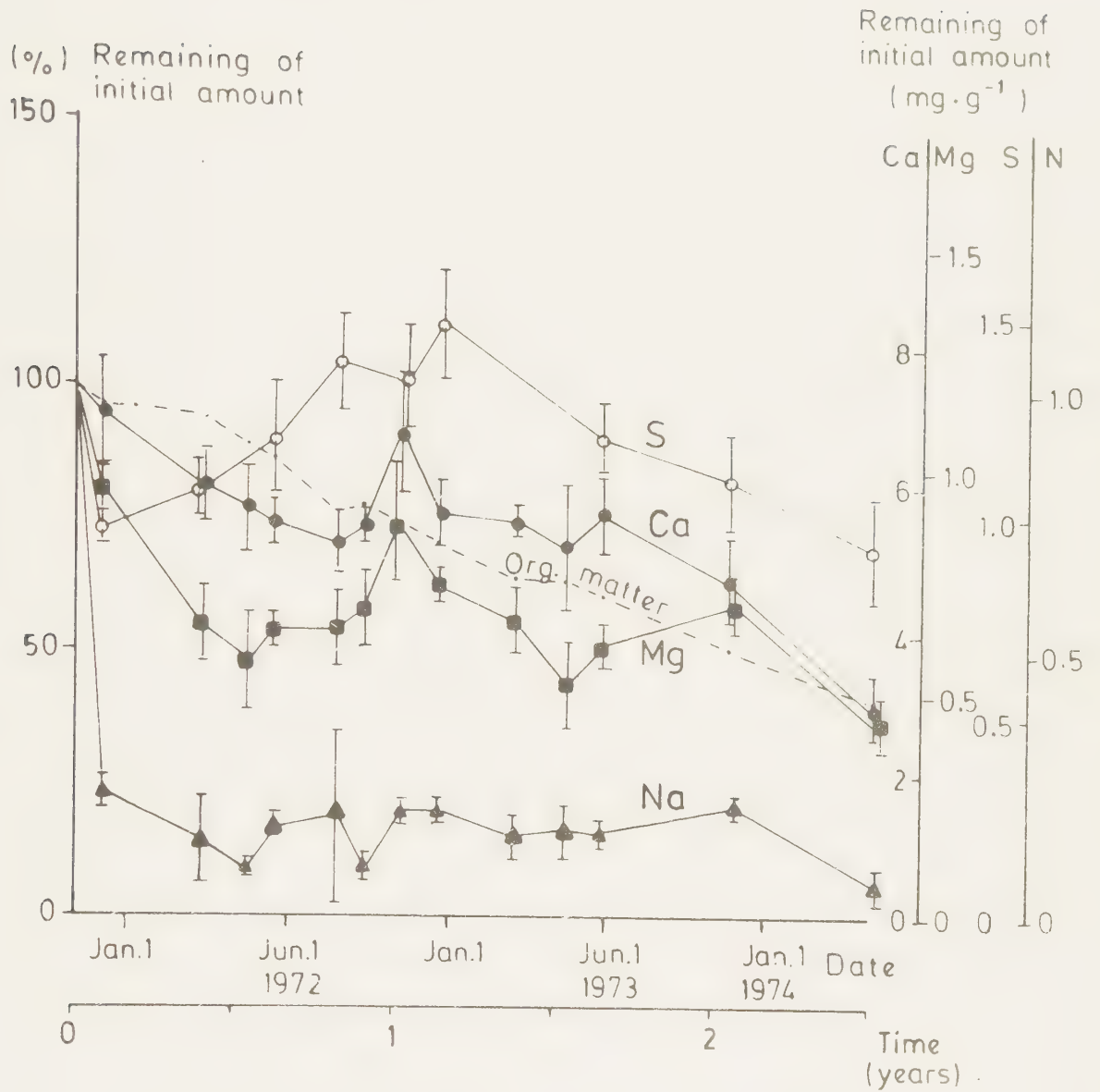


Figure 1 (continued)

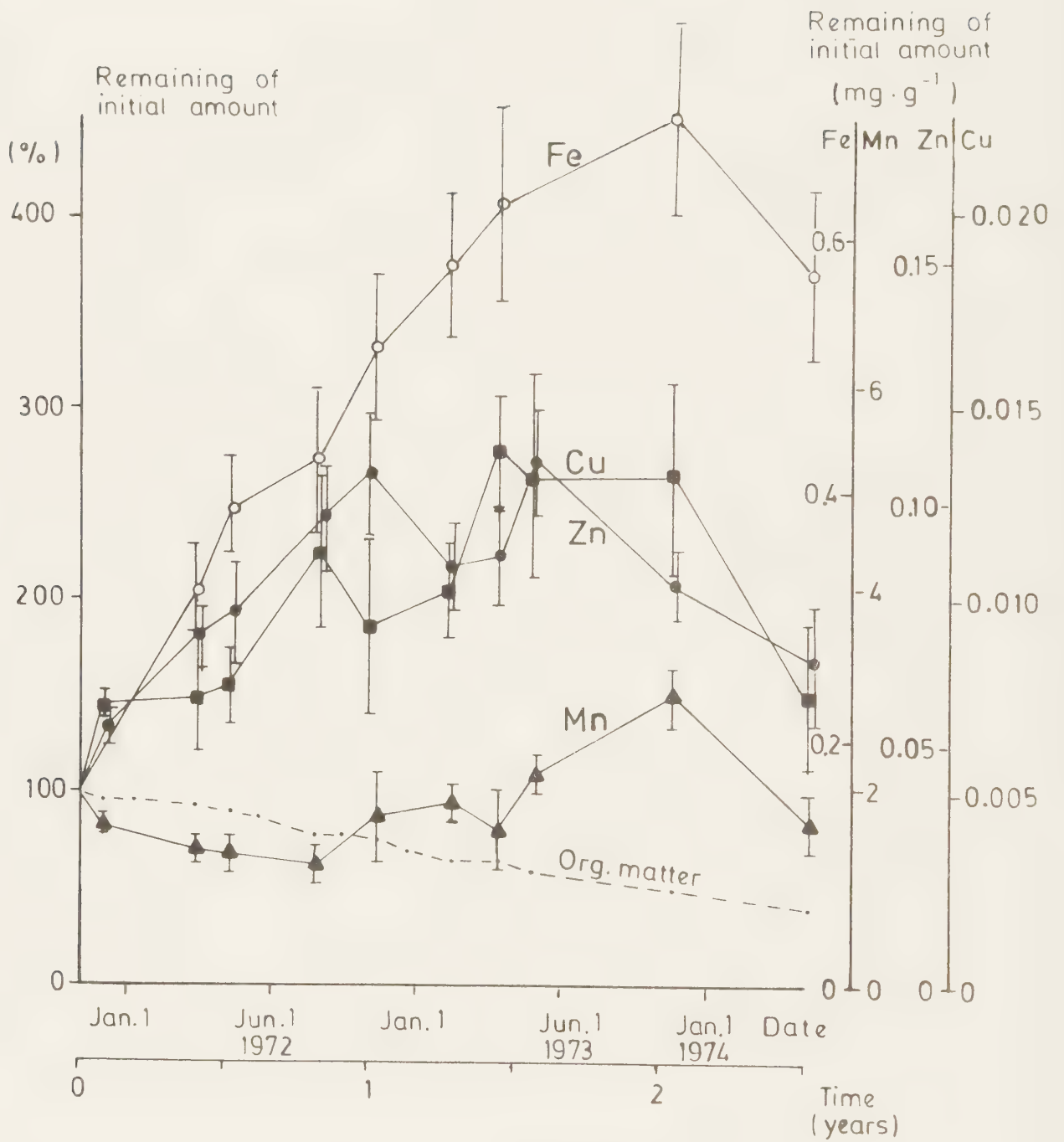


Figure 1 (continued)

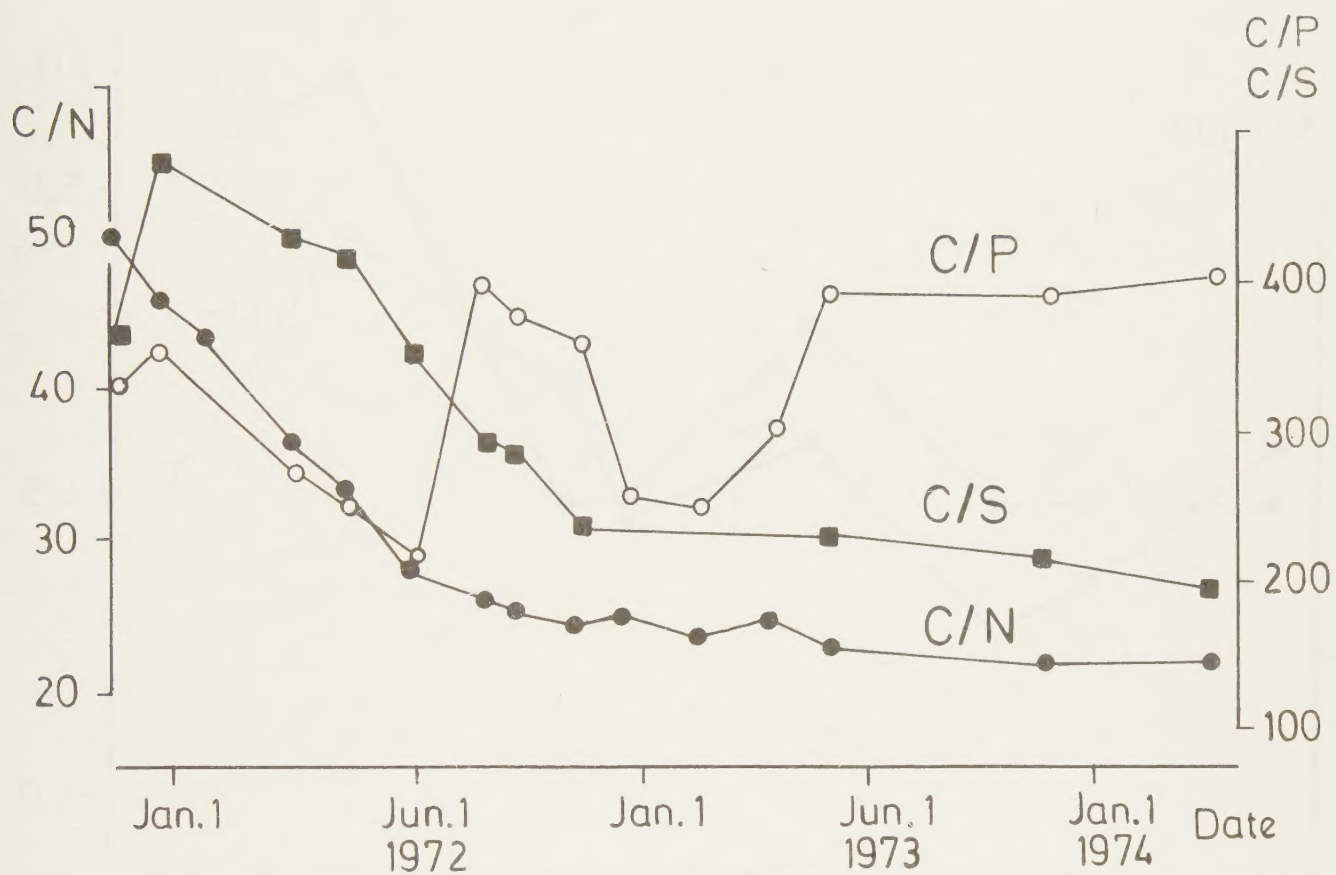


Figure 2. Carbon/element ratios for nitrogen, phosphorus and sulphur in decomposing beech leaf litter. The measurements were made using litter bags at the Kongalund site, and started in Nov. 1971.

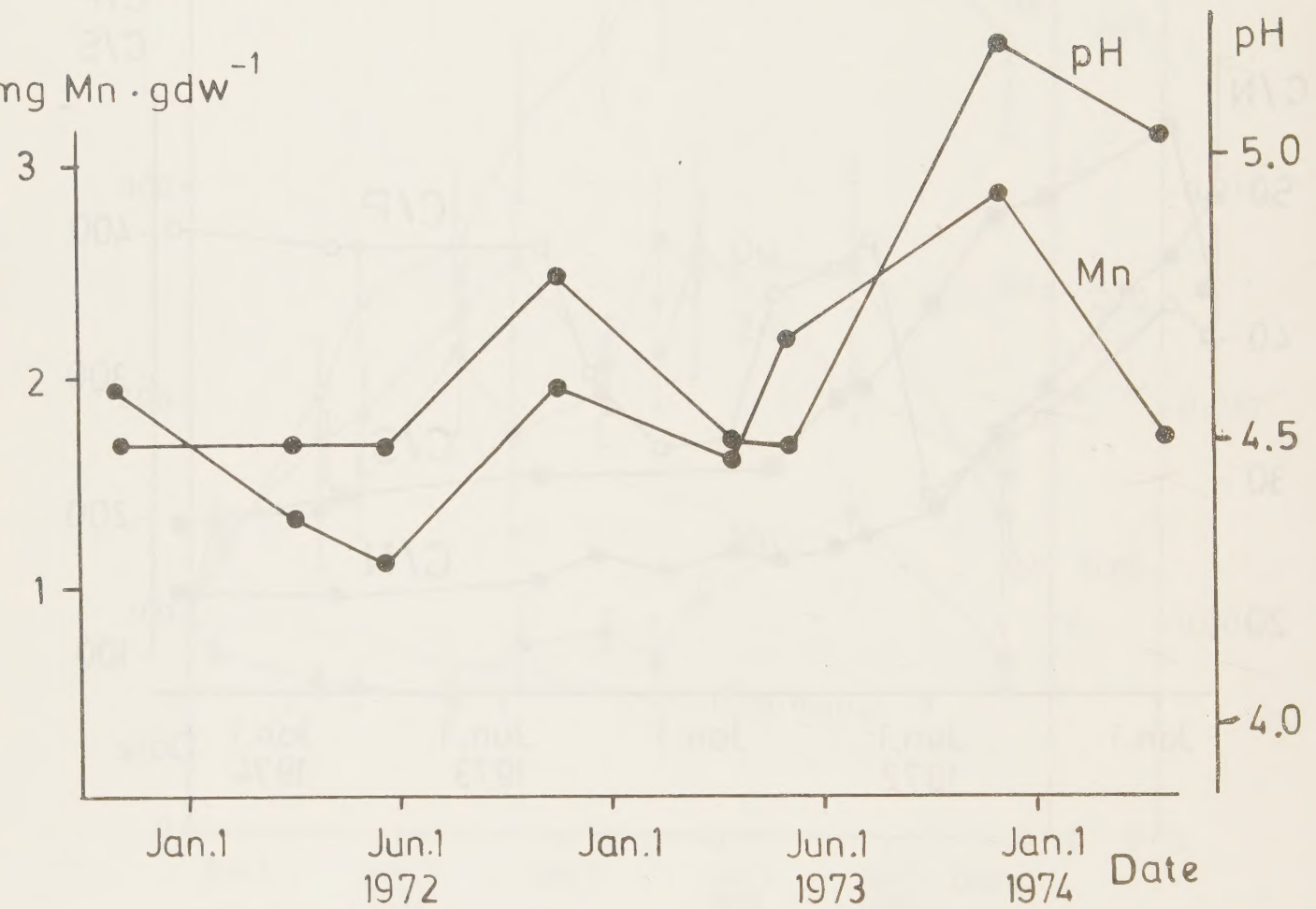


Figure 3. Change in pH on water extracts from and remaining manganese amounts in decomposing beech leaf litter. The experiment was laid out in Kongalund in November 1971.

